Chapter 7

Amphibians and Reptiles of the Anjanaharibe-Sud Massif, Madagascar: Elevational Distribution and Regional Endemicity

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Abstract

Before 1994 the Anjanaharibe-Sud Massif, including the Réserve Spéciale (RS) d'Anjanaharibe-Sud, had never been surveyed for amphibians and reptiles. During the rainy seasons of 1994 and 1996, surveys were made on the eastern and western slopes of the massif in moist and sclerophyllous montane forest between 800 and 2000 m elevation. Fifty-three species of amphibian and 40 species of reptile were recorded. Most of the species (89%) are restricted to rain forest, and five species appear to be endemic to the Anjanaharibe-Sud Massif. Although species diversity is similar on both the eastern and western slopes (at similar elevations), 30 species are restricted to a single slope only (between 1000 and 1700 m elevation), suggesting significant differences in community composition. Species diversity of both amphibians and reptiles declines with increasing elevation. A large component of the montane herpetofauna of the RS d'Anjanaharibe-Sud (above 1500 m elevation) also occurs on the massifs of Marojejy (74%) and Tsaratanana (74%). Considering all elevations, the herpetofauna of the RS d'Anjanaharibe-Sud is most similar to that of the Réserve Naturelle Intégrale (RNI) de Marojejy (64%). However, 22 species found in the RS d'Anjanaharibe-Sud that have widespread distributions in eastern Madagascar are not known in the RNI de Marojejy. Two barriers to dispersal are suggested between the Anjanaharibe-Sud and Marojejy massifs, the Androranga and Lokoho rivers. The rich species diversity, potential local endemicity, and unique biogeographic affinities to both the eastern and northern regions all demonstrate the importance of the RS d'Anjanaharibe-Sud within the protected area network of Madagascar.

Résumé

L'inventaire des amphibiens et des reptiles du massif d'Anjanaharibe-Sud, qui comprend la Réserve Spéciale (RS) d'Anjanaharibe-Sud, n'avait jamais été réalisé auparavant. Au cours de la saison des pluies des années 1994 et 1996, des inventaires ont été conduits sur les versants orientaux et occidentaux du massif, au sein de la forêt humide sempervirente de moyenne et de haute altitudes, entre 800 et 2000 m. Un total de 53 espèces d'amphibiens et de 40 espèces de reptiles a été répertorié. La majorité des espèces (89%) était restreinte à la forêt pluviale et

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cing espèces semblent êntre endémiques du massif d'Anjanaharibe-Sud. Bien que la diversité spécifique soit équivalente entre les versants occidentaux et orientaux, à altitude équivalente, 30 espèces se rencontrent uniquement sur un seul versant, entre 1100 et 1700 m d'altitude, suggérant qu'il existe des différences importantes dans la composition des communautés d'amphibiens et de reptiles. La diversité spécifique des amphibiens et des reptiles diminue en fonction de l'augmentation de l'altitude. Une proportion importante de l'herpétofaune de la zone d'altitude de la RS d'Anjanaharibe-Sud (au-dessus de 1500 m) se rencontre également dans le massif du Marojejy (74%) et dans le massif du Tsaratanana (74%). En prenant en compte toutes les stations altitudinales inventoriées, la RS d'Anjanaharibe-Sud est similaire à la Réserve Naturelle Intégrale (RNI) de Marojejy (64%). Cependant, 22 espèces rencontrées dans la RS d'Anjanaharibe-Sud n'ont pas été inventoriées au sein de la RNI de Marojejy, alors qu'elles ont par ailleurs une distribution étendue au sein de la forêt pluviale de l'est de Madagascar. Les deux barrières naturelles à l'origine de la différence dans la distribution des espèces de reptiles et d'amphibiens pourraient être les rivières Androranga et Lokoho. La riche diversité spécifique, le potentiel d'endémisme local et les relations biogéographiques exceptionnelles vis à vis des régions du nord et de l'est de Madagascar démontrent l'importance de la RS d'Anjanaharibe-Sud dans le contexte du réseau d'aires protégées de Madagascar.

Introduction

The Anjanaharibe-Sud Massif in northern Madagascar (14°42′S, 49°26′E) is a north-south-oriented ridge about 20 km long with three summits between 1899 and 2064 m elevation. The primary vegetation of the massif is moist and sclerophyllous montane forest. Anjanaharibe-Sud is close to two major massifs in Madagascar, 45 km southwest of Marojejy, and 90 km southeast of Tsaratanana. The Anjanaharibe-Sud Massif does not have an extensive montane heathland (although the extreme summit above 1950 m does include a small area of heathland) and in this respect is unlike Marojejy and Tsaratanana, both of which have this vegetation type above 2000 m elevation. The 32,100 ha Réserve Spéciale (RS) d'Anjanaharibe-Sud, established in 1958, protects forest of the massif between 500 and 2064 m elevation (Nicoll & Langrand, 1989).

Before this study, no collections of amphibians and reptiles had been made in the Anjanaharibe-Sud region or reserve and the only published herpetological data consisted of a field observation of a single gecko species (Nicoll & Langrand, 1989). This contrasts with the nearby Réserve Naturelle Intégrale (RNI) de Marojejy, which was surveyed for amphibians and reptiles in the early 1970s (Guillaumet et al., 1975) and was subsequently surveyed by other herpetologists (Glaw & Vences, 1994; Raxworthy & Nussbaum, 1997).

During October and November 1994, as part of a multidisciplinary study, a herpetological survey was made of the highest summit and eastern side of the RS d'Anjanaharibe-Sud at the start of the rainy season. This inventory was further enriched by a subsequent herpetological survey completed on the western side of the massif, which was made during January and February 1996, at the peak of the rainy season.

Study Sites

Field work was centered on six elevational transects, four on the eastern slope of the massif (in the Lokoho River basin), with the highest elevation transect also including the ridge, and two on the western slope (in the Antainambalana River basin).

Eastern Transects E1

E1—14°45.3′S, 49°30.3′E. Survey dates: 18–30 October 1994. Sampling days: 13. Altitude surveyed: 800–950 m. Habitat: primary to slightly disturbed moist montane forest.

E2—14°44.7′S, 49°27.7′E. Survey dates: 1–12 November 1994. Sampling days: 12. Altitude surveyed: 1100–1350 m. Habitat: primary moist montane forest.

E3—14°44.5′S, 49°26.5′E. Survey dates: 14–23 November 1994. Sampling days: 10. Altitude surveyed: 1500–1700 m. Habitat: primary moist montane forest.

Eastern and Ridge Transects

E4—14°44.8′S, 49°25.0′E. Survey dates: 24–28 November 1994. Sampling days: 5. Altitude surveyed: 1850–2000 m. Habitat: primary sclerophyllous montane forest mixed with areas dominated by bamboo and ericoid shrubs.

Western Transects

W1—14°46′S, 49°27′E. Survey dates: 25 January–3 February 1996. Sampling days: 10. Altitude surveyed: 1000–1100 m. Habitat: primary moist montane forest.

W2—14°46′S, 49°26′E. Survey dates: 5–11 February 1996. Sampling days: 7. Altitude surveyed: 1200–1600 m. Habitat: primary moist montane forest.

Materials and Methods

The four members of the herpetological field survey team were N. Rabibisoa (eastern survey), F. Andreone (western survey), H. Randriamahazo (western survey), and J. E. Randrianirina (western survey).

The surveys were done either during the start (October–November) or middle (January–February) of the rainy season, when species are breeding and activity is at its highest. Field techniques used to sample animals (by both day and night) were as follows: (1) pitfall trapping with drift fences, (2) visual and acoustic searching, and (3) refuge examination (under and in fallen logs and rotten tree stumps; under bark; under rocks; in leaf litter, root-mat, and soil; and in leaf axils of *Pandanus* screw palms and *Ravenala* traveler's palm).

The pitfall traps were buckets (275 mm deep, 290 mm top internal diameter, and 220 mm bottom internal diameter) with the handles removed and small holes (2 mm diameter) punched in the bottom to allow water drainage. Buckets were sunk into the ground along a drift fence made from plastic sheeting (0.5 m wide) stapled in a vertical position to thin wooden stakes, with the fence bottom sealed 50 mm deep into the ground using soil and leaf litter. The trap lines were checked each morning and late afternoon. After heavy rain, the traps were sponge-dried.

For the eastern transects, the drift fence (100 m in length) was positioned to run across the middle of each pitfall trap. Pitfall traps were positioned at both ends of the drift fence, with the other nine traps at 10 m intervals. Three lines were used, placed in the following forest types: ridge (along the crest of a ridge), slope (on a gradient, intermediate between ridge top and valley bottom), and valley (within 20 m of a stream in a valley bottom). This procedure was used on previous surveys (e.g., Raxworthy & Nussbaum, 1994, 1996b) and is recommended for use on future projects to allow standardization of capture techniques and subsequent comparisons of results.

For the western transects, pitfalls were placed adjacent to the drift fence, alternating on each side of the fence, and at each end, at 5 m intervals. Three lines 50 m long were used at the 1050 m transect, with 11 pitfalls per line. Two lines 60 m long were used at the 1400 m transect, with 13 pitfalls per line.

Visual searches and refuge examinations were made throughout the full elevation range of habitats available in the reserve. The majority of searching was done close to trails made during the study, although ridges and riverbanks were also used to orient search paths. Night searches were made using headlights.

The following information was recorded at the time of capture for each individual: date, time, longitude, latitude, altitude, microhabitat, and circumstances of capture. Animals not retained for specimens were returned to the site of original capture. Voucher specimens were fixed in 10% buffered formalin and later transferred to alcohol. Color slides were taken of representative live individuals of many species. Frog calls were recorded when possible. Collected material was deposited at four research collections: for the eastern survey, at the Département de Biologie Animale, Université d'Antananarivo, and the Museum of Zoology, University of Michigan; and for the western survey, at the Section de Zoologie, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, and the Museo Regionale di Scienze Naturali, Torino.

Results

Fifty-three amphibian and 40 reptile species were recorded at the RS d'Anjanaharibe-Sud (Table 7-1), including two subspecies and six amphibians and four reptiles that may represent new

Table 7-1. Amphibians and reptiles recorded from the RS d'Anjanaharibe-Sud.

Species	Transect*					
	E1 800–950 m	E2 1100–1350 m	E3 1500–1700 m	E4 1850–2000 m	W1 1000–1100 m	W2 1200–1600 m
AMPHIBIA						
MICROHYLIDAE						
Anodonthyla boulengeri				*	*	
Platypelis grandis	*	*			*	*
Platypelis cf. *occultans*					*	*
Platypelis pollicaris	*	*	*			
Platypelis tsaratananaensis			*	*		*
Platypelis tuberifera		*				*
Platypelis sp. 1		*	*			
Platypelis sp. 2		*				*
Platypelis sp. 3						*
Plethodontohyla laevipes		*				
Plethodontohyla minuta	*		*			
Plethodontohyla notosticta			*		*	*
Plethodontohyla serratopalpebrosa		*	*	*	*	*
Plethodontohyla sp. 1			*	*	*	
Plethodontohyla sp. 2	?	?	?	?		
Stumpffia grandis	*					
Stumpffia roseifemoralis	*	*	*			*
Stumpffia tetradactyla					*	*
RANIDAE						
Ptychadena mascareniensis	*					
MANTELLIDAE[†]						
Mantella sp. 1	*				*	
Mantidactylus aglavei	*	*			*	*
Mantidactylus albofrenatus	*	*	*		*	*
Mantidactylus asper		*			*	*
Mantidactylus betsileanus	*	*			*	
Mantidactylus bicalcaratus	*	*	*	*	*	*
Mantidactylus biporus	*	*				
Mantidactylus cornutus		*	*	*	*	*
Mantidactylus elegans				*		
Mantidactylus femoralis	*	*	*		*	
Mantidactylus flavobrunneus	*	*				
Mantidactylus grandidieri					*	
Mantidactylus grandisonae		*			*	*
Mantidactylus guttulatus		*				
Mantidactylus liber		*	*		*	
Mantidactylus luteus	*	*			*	
Mantidactylus opiparis		*			*	
Mantidactylus peraccae		*	*		*	*
Mantidactylus pulcher	*	*				*
Mantidactylus rivicola		*	*		*	
Mantidactylus redimitus	*				*	
Mantidactylus ulcerosus		*				
RHACOPHORIDAE[†]						
Aglyptodactylus madagascariensis				*	*	*
Boophis albilabris					*	
Boophis cf. *albipunctatus*		*				
Boophis cf. *brachychir*	*		*		*	*
Boophis erythrodactylus					*	
Boophis luteus cf. *septentrionalis*					*	
Boophis madagascariensis		*			*	
Boophis mandraka		*			*	
Boophis marojezensis		*	*		*	
Boophis rappiodes					*	
Boophis reticulatus	*	*	*		*	*
Boophis anjanaharibeensis					*	

TABLE 7-1. *Continued.*

Species	Transect					
	E1 800–950 m	E2 1100–1350 m	E3 1500–1700 m	E4 1850–2000 m	W1 1000–1100 m	W2 1200–1600 m
REPTILIA						
GEKKONIDAE						
Ebenavia inunguis	*					
Phelsuma guttata	*					
Phelsuma lineata	*	*				
Phelsuma quadriocellata	*	*				
Paroedura gracilis		*				*
Uroplatus cf. *ebenaui*		*			*	*
Uroplatus sikorae	*					
CHAMAELEONIDAE						
Brookesia betschi					*	*
Brookesia therezieni	*					*
Brookesia vadoni						*
Calumma brevicornis		*	*	*	*	*
Calumma gastrotaenia guillaumeti		*	*		*	*
Calumma gastrotaenia marojezensis	*					
Calumma malthe		*	*			
Calumma nasuta	*	*	*		*	*
Calumma parsoni		*			*	*
Furcifer pardalis	*					
SCINCIDAE						
Amphiglossus melanopleura			*			
Amphiglossus melanurus	*				*	*
Amphiglossus minutus	*	*			*	*
Amphiglossus mouroundavae						*
Amphiglossus punctatus		*				*
Amphiglossus cf. *tsaratananaensis*					*	*
Androngo crenni					*	
Mabuya gravenhorstii	*					
Paracontias hildebrandti					*	
CORDYLIDAE						
Zonosaurus madagascariensis	*	*			*	
BOIDAE						
Boa manditra	*	*				
TYPHLOPIDAE						
Typhlops mucronatus					*	
COLUBRIDAE						
Brygophis coulangesi						*
Geodipsas infralineata	*				*	
Geodipsas sp. 1			*	*		
Liophidium rhodogaster	*					*
Liophidium sp. 1	*					
Liophidium sp. 2	*					
Liopholidophis epistibes	*					
Liopholidophis infrasignatus						*
Lycodryas betsileanus	*					
Pseudoxyrhopus microps		*				
Pseudoxyrhopus tritaeniatus					*	
Pseudoxyrhopus sp. 1					*	
Total species	39	45	24	10	50	38

* E = eastern transects; W = western transects.

† The taxonomic rank of mantellines and rhacophorines is still uncertain. Most recently authors have considered them as either families (Blommers-Schlösser & Blanc, 1991) or subfamilies of Ranidae (Blommers-Schlösser, 1993; Glaw & Vences, 1994). Here we tentatively continue to give them the status of families.

taxa. In addition, another new species of amphibian, *Boophis anjanaharibeensis*, has now been described by Andreone (1996). A similar degree of species diversity (sometimes termed species richness; see Rosenzweig 1995:201, who recommends that this term be abandoned) was recorded on both sides of the massif: amphibian species, 44 east, 40 west; and reptile species, 29 east, 24 west. Species diversity was greatest at the lower elevation transects: 34 species of amphibians at transect W1 and 20 species of reptiles at transect E1. Species diversity was lowest at the highest transect (E4) for both amphibians (eight species) and reptiles (two species) (Table 7-1, Fig. 7-1).

The pitfall data are given in Tables 7-2 and 7-3. Eight amphibian and nine reptile species were captured in pitfall traps, among a sample of 30 individuals, during 1,458 trap-days. Overall pitfall capture success was 2% daily for amphibians and reptiles.

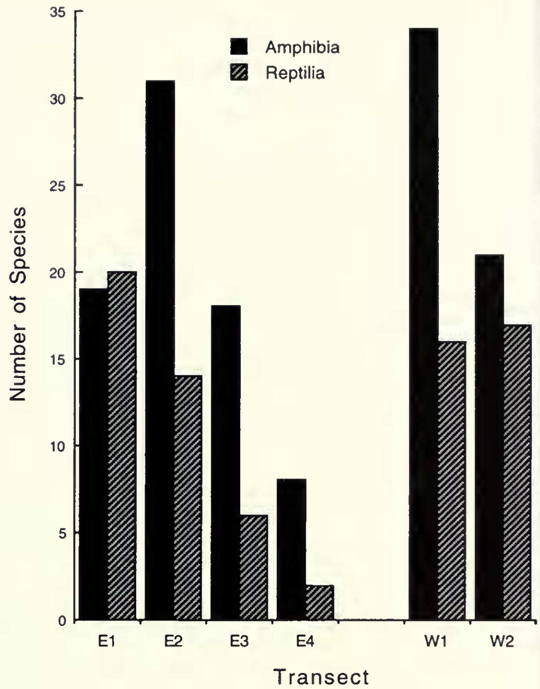

FIG. 7-1. Herpetofaunal diversity in each transect zone within the RS d'Anjanaharibe-Sud.

Discussion

Species Not Found

Nicoll and Langrand (1989) listed *Uroplatus fimbriatus* for the RS d'Anjanaharibe-Sud, a gecko we did not find during our surveys. It seems probable that this record is based on a personal observation without vouchers, because the most recent revision of *Uroplatus* (Bauer & Russell, 1989) does not list *Uroplatus* museum material for RS d'Anjanaharibe-Sud. We strongly suspect that this record of *U. fimbriatus* actually represents a misidentified *U. sikorae* (a species resurrected from synonymy with *U. fimbriatus* by Bauer & Russell, 1989), which we recorded at the lowest elevational transect (E1) on the eastern slopes of the RS d'Anjanaharibe-Sud.

Sampling

The herpetological capture success of the pitfall traps, 30 captures in 1,458 trap-days (2.1% daily trap success), is almost half that achieved by pitfall traps at RNI d'Andringitra, where 32 herpetological captures were made in 902 trap-days (3.5% daily trap success) (Raxworthy & Nussbaum, 1996b).

At the RS d'Anjanaharibe-Sud, pitfall capture success was especially poor for the eastern transects; just 13 individuals were caught in 1,045 trap-days (1.2% daily trap success) using a trapping method identical to that used at RNI d'Andringitra. It is not clear whether species susceptible to pitfall trapping are less abundant at the RS d'Anjanaharibe-Sud or whether lower trap rates might reflect seasonal differences in activity (pitfall trapping at the RNI d'Andringitra started 29 days later than at RS d'Anjanaharibe-Sud).

For the western transects, pitfall success was much higher: 17 individuals in 413 trap-days (4.1% daily trap success). However, these results are not directly comparable with those from RNI d'Andringitra because different pitfall sampling methods were used.

By the end of each transect sampling period, few species not previously recorded in the zone were being discovered for the eastern transects (Fig. 7-2), with the last day of surveying producing only 0–2 additional species per transect.

For the eastern transects, based on the species-accumulation curves, the best surveyed transects are E1 (800–950 m) and E3 (1500–1700 m), where just one additional species was found over the last 3 days of surveying. However, the sampling periods of 12 days at E2 (1100–1350 m)

TABLE 7-2. Characteristics and herpetological capture results for all pitfall lines.

Character	East Lines												West Lines				
	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5
Descriptive																	
Altitude, m	890	850	850	1250	1230	1240	1550	1510	1500	1970	1930	1950	1060	1060	1060	1370	1440
Forest type*	R	V	S	R	V	S	R	V	S	R	V	S	V	S	R	S	S
Dates (day/month)																	
Start	19/10	19/10	20/10	4/11	4/11	4/11	15/11	15/11	15/11	24/11	24/11	24/11	29/1	29/1	29/1	6/2	6/2
End	28/10	28/10	28/10	10/11	10/11	10/11	21/11	21/11	21/11	30/11	30/11	30/11	3/2	3/2	3/2	12/2	12/2
Total trap-days	110	110	99	88	88	88	88	77	77	77	77	77	77	77	77	91	91
Results																	
Total captures	0	5	0	1	1	3	1	0	0	1	1	0	7	3	1	5	1
Total species	0	4	0	1	1	1	1	0	0	1	1	0	3	3	1	5	1
Daily capture success, %	0	5	0	1	1	3	1	0	0	1	1	0	9	4	1	5	1

* R = ridge; S = slope; V = valley.

and 5 days at E4 (1850–2000 m) were probably too short for a single researcher to make a complete survey, as five and three species, respectively, were found over the last 2 days of sampling.

For the western transects, three researchers worked over a 7- to 10-day period, compared with a single collector at the eastern transects. The greater collecting intensity in the western transects is reflected by the much greater rate of species acquisition during the first 2 days at each transect. By the final 2 days of surveying, only two additional species were sampled at W2 (1200–1600 m), but a diversity plateau was not evident at W1 (1000–1100 m), suggesting that surveying time was too short.

Elevational Distribution

Only one species, *Mantidactylus bicalcaratus*, a *Pandanus* screw palm frog, is distributed across the entire elevational range of all six transects (890–1950 m). Six amphibian species are found between E1 and E3 (950–1500 m), and three species are found between E2 and E4 (1350–1850 m). The reptiles appear to be more restricted in their elevational tolerance, with just two species occurring in three adjoining eastern transect zones. Both are chameleons: *Calumma brevicornis* (1300–1950 m) and *C. nasuta* (875–1580 m).

Despite the significant turnover in species with elevation in the RS d'Anjanaharibe-Sud, only two vegetation types are recognized within the survey transects: moist montane forest, typically between 800 and 1300 m, and sclerophyllous montane rain forest, typically between 1300 and 2000 m (White, 1983; Jenkins, 1987). The boundary between moist and sclerophyllous montane forest is actually difficult to determine because the two forest types intergrade (Raxworthy & Nussbaum, 1996a); in the RS d'Anjanaharibe-Sud, trees with sclerophyllous leaves were recorded only at the highest-elevation transect, 1850–2000 m. Surprisingly, herpetofaunal endemism is extremely low in this habitat, with only one species, *Mantidactylus elegans*, restricted to sclerophyllous forest on the Anjanaharibe-Sud Massif. This compares to 18 species (7 amphibians and 11 reptiles) restricted to moist montane forest below 1100 m elevation (rain forest endemics distributed in E1 and W1 only). The turnover of amphibians and reptiles in moist montane forest in the RS d'Anjanaharibe-Sud suggests that this single habitat type actually has several herpetological com-

TABLE 7-3. Herpetological capture results for all pitfall lines.

Species	East Lines												West Lines					Total Captures
	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	
AMPHIBIA																		
Platypelis grandis		1																1
Plethodontohyla notosticta																	1	1
Plethodontohyla serratopalpebrosa											1			1				2
Plethodontohyla sp. 1.											1							1
Stumpffia roseifemoralis		1																1
Mantidactylus asper													1					1
Mantidactylus opiparis														1				1
Mantidactylus redimitus		1																1
REPTILIA																		
Amphiglossus melanopleura							1											1
Amphiglossus melanurus																1		1
Amphiglossus minutus		1											5			1		7
Amphiglossus mouroundavae																1		1
Amphiglossus punctatus				1	1	3										1		6
Amphiglossus cf. *tsaratananaensis*															1	1		2
Androngo crenni														1				1
Liophidium rhodogaster		1																1
Pseudoxyrhopus sp. 1													1					1
Total	0	5	0	1	1	3	1	0	0	0	2	0	7	3	1	5	1	30

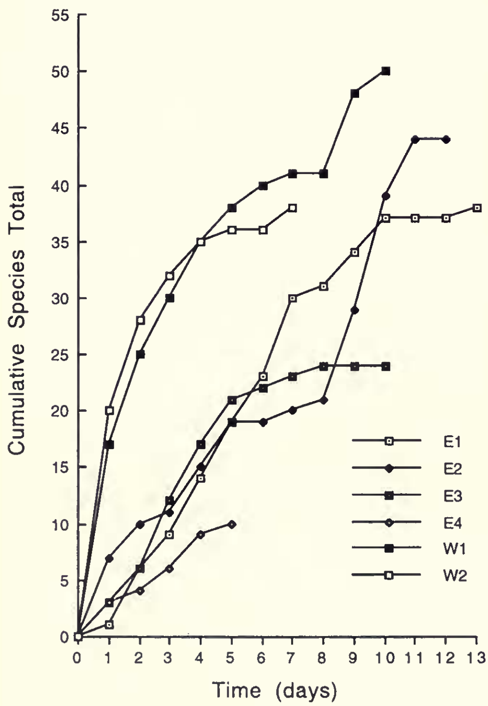

FIG. 7-2. Accumulation curves of herpetofaunal diversity (all sampling techniques) in each transect zone within the RS d'Anjanaharibe-Sud.

munities, each adapted to a narrower elevational range.

A 900 m transition in rain forest herpetofaunal communities was reported at Montagne d'Ambre (Raxworthy & Nussbaum, 1994). In the RS d'Anjanaharibe-Sud, this transition occurs between the E1 transect (800–950 m) and the higher elevation transects. A total of 12 species are restricted to below 950 m, 54 species are restricted to above 1000 m, and 26 species occur both above and below 950 m.

A summary of species diversity for each transect is shown in Figure 7-1. Amphibian species diversity declines above 1500 m elevation in the eastern transects and above 1200 m in the western transects. The amphibian species diversity for the lowest elevation transect, E1 (800–950 m), is lower than for the midelevation transect, E2, indicating a midelevation diversity bulge. For reptiles, there is an obvious negative relationship between elevation and species diversity in the eastern transects, but the two western transects have almost the same species diversity despite their different elevations.

These results are similar to elevational species diversity trends reported for the RNI d'Andringitra by Raxworthy and Nussbaum (1996b). On the Andringitra Massif, there is an obvious general decline in species diversity at higher elevation, above the lowest elevation transect of 650–800 m for reptiles and above the second lowest elevation transect of 750–860 m for amphibians. Species diversity of both amphibians and reptiles is less than 10 species at transects above 1850 m elevation for both the Andringitra and Anjanaharibe-Sud Massifs.

There is no doubt that herpetofaunal species diversity decreases in montane regions of Madagascar (above 1500 m), but the factors responsible for this decline are unknown. A midelevation diversity bulge in species diversity was reported at the RNI d'Andringitra for amphibians (Raxworthy & Nussbaum, 1996b) and is also evident for amphibians on the Anjanaharibe-Sud Massif. Because trends in species diversity at low elevation (below 700 m) have not been described (largely because so little forest of this type still survives in Madagascar), it is not clear whether the midelevation diversity bulge also exists for reptiles. If this is the case, maximum reptile species diversity will occur at a lower elevation than that recorded for amphibians.

Elevational diversity gradients in general remain poorly understood, but tropical, midelevation diversity bulges have now been reported for bryophytes (Gradstein & Pocs, 1989), pteridophytes (Tryson, 1989), arthropods (Janzen et al., 1976), birds (Terborgh, 1977), and mammals (Heaney & Rickart, 1990). These patterns all appear to represent the unimodal productivity pattern of species diversity, which has been most recently reviewed by Rosenzweig (1995). Theories for the decrease phase (decreasing species diversity with higher productivity, such as at lower elevations) remain controversial, and none has yet gained widespread acceptance.

Eastern and Western Slopes

Table 7-1 shows obvious differences between the eastern and western transects of similar elevations. Comparisons made between the herpetofauna of transect E2 + E3 (1100–1700 m) and W1 + W2 (1000–1600 m) reveal 11 species found only on the eastern side and 19 species found only on the western side. Although these differences are large, interpretation of this result is complicated by the timing of the eastern and western surveys at different periods of the rainy season. Because changes in herpetofaunal species activity are typically not obvious between the start and middle of the rainy season (unlike the dramatic changes in activity that occur between the dry and rainy seasons), we consider it unlikely that survey timing could account for all sampling differences between the forests of the eastern and western flanks of the Anjanaharibe-Sud Massif.

Other possible explanations for these east-west differences concern the pitfall trapping methods used and the field collectors, which were not identical for the eastern and western forests surveys. If the pitfall trap data are removed from the analysis, this accounts for east-west differences in only four species: *Amphiglossus mouroundavae*, *Amphiglossus* cf. *tsaratananaensis*, *Androngo crenni*, and *Pseudoxyrhopus* sp. 1.

Although identical collecting methods were used, collecting ability inevitably varies among individuals. Incomplete surveying by collectors always produces a taxonomic bias toward those groups most frequently encountered and easy to capture. The species collected on the eastern and western transects do not indicate taxonomic bias toward easy-to-capture groups because cryptic groups such as microhylids (*Plethodontohyla*, *Platypelis*, and *Stumpffia*), chameleons (*Brookesia* and *Calumma*), and fossorial/semifossorial skinks (*Amphiglossus*) and snakes (*Pseudoxyrhopus*) are represented in both collections. Thus, differences in collecting ability among collectors are not obvious between the eastern and western transects.

Another potential sampling problem is that all of the transects appear not to have been surveyed for a sufficient period of time to ensure that all species were sampled (Fig. 7-2).

Although there may have been sampling biases that could account for some of the differences, we suspect that real differences exist between the herpetofaunal communities on the eastern and western flanks of the Anjanaharibe-Sud Massif. The differences are too great to be explained by sampling bias alone.

East-west herpetofaunal difference may result from the north-south orientation of the massif and the effect this orientation has on local climate. For much of the year, trade winds blow across Madagascar from the east (Donque, 1972), creating rain shadows on the western slopes of some massifs. (The most striking rain shadow we have observed occurs on the western flank of the Anosy Mountains, where moist montane forest and arid spiny forest may be separated by as little as 3 km.) In addition, solar radiation is unlikely to be the same on the east- and west-facing slopes. Differences in precipitation and solar radiation will certainly have significant effects on the habitats on the eastern and western slopes and therefore are also likely to result in different herpetofaunal communities.

Regional Endemicity

Endemism of amphibians and reptiles at RS d'Anjanaharibe-Sud is summarized in Table 7-4. Most (89%) of the species are endemic to rain forest habitats in Madagascar. Those species not endemic to rain forest (moist and sclerophyllous) appear to be tolerant of human disturbance and are able to survive in agricultural or urban environments. None of these species is a specialist of the arid habitats that occur in southern and western Madagascar.

Two sites in close proximity to Anjanaharibe-Sud Massif were selected for regional comparison: Tsaratanana, 14°26′S, 49°46′E (90 km northwest of Anjanaharibe-Sud), and Marojejy, 14°11′S, 48°57′S (45 km northeast of Anjanaharibe-Sud). The Tsaratanana and Marojejy massifs are especially appropriate for comparison because both are montane rain forest sites with the same habitats as Anjanaharibe-Sud. Both sites are included in reserves (described in detail by Nicoll & Langrand, 1989) and were surveyed for amphibians and reptiles between 1992 and 1993 as part of a major rain forest survey in Madagascar (see Raxworthy & Nussbaum, 1997). The surveyed Marojejy rain forest includes the same elevational range as Anjanaharibe-Sud. In the surveyed region at Tsaratanana, rain forest below 1500 m was either heavily degraded or reduced to small fragments. Therefore, primary forest of this elevation could not be adequately surveyed.

Table 7-4 lists the species found at Anjanaharibe-Sud Massif that also occur on the Tsaratanana and Marojejy massifs. The majority of Anjanaharibe-Sud species (64%) are also found at Marojejy, compared with Tsaratanana, where only 36% of the Anjanaharibe-Sud herpetofauna is distributed. As expected, there is a close similarity between the Marojejy and Anjanaharibe-Sud herpetofaunas.

The smaller fraction of Anjanaharibe-Sud species shared with Tsaratanana, however, is misleading. This reflects the absence of lower elevation forest (below 1500 m) at Tsaratanana. Thus, lower elevation Anjanaharibe-Sud species such as *Platypelis grandis*, *Plethodontohyla laevipes*, *Mantella* sp. 1, *Boophis madagascariensis*, *Paroedura gracilis*, and *Uroplatus sikorae*, which are known both east and west of the Tsaratanana Massif (Raxworthy & Nussbaum, unpubl. data), probably would have been recorded at Tsaratanana if lower elevation forest still existed at the survey site. However, the absence of some species at Tsaratanana that have a broad elevational range at Anjanaharibe-Sud (*Anodonthyla boulengeri*, *Mantidactylus bicalcaratus*, and *Mantidactylus cornutus*) suggests real biogeographic differences in the faunas of each massif.

A biogeographic comparison restricted to just the Anjanaharibe-Sud species recorded above 1500 m (transects E3 and E4) includes 27 species: 21 amphibians and 6 reptiles, all 27 of which are known from either Tsaratanana or Marojejy. Of these 27 montane Anjanaharibe-Sud species, 20 species (74%) occur at Tsaratanana and 20 species (74%) occur at Marojejy. The montane herpetofauna of Anjanaharibe-Sud is, therefore, equally similar to what is found on both these other massifs, despite the proximity of Anjanaharibe-Sud to Marojejy.

Five species recorded at Anjanaharibe-Sud are currently unknown from any other site and therefore are considered here to be endemic to the massif (Table 7-4). It seems likely that some or all of these species have a genuinely small distribution confined to the Anjanaharibe-Sud Massif because they have not been found during herpetofaunal surveys by us or others at other sites in the region.

The elevational ranges of all five potential endemics fall between 800 and 1600 m; and none is a high-elevation specialist (restricted to above 1500 m, see Raxworthy & Nussbaum, 1996a). This is surprising, because the forest of Anjanaharibe-Sud Massif, below 1500 m, extends continuously northward via Betaolana to Marojejy and via Andramanalana to Tsaratanana. Surveys at Betaolana and Andramanalana would determine whether these presumed Anjanaharibe-Sud endemics are actually restricted to the massif. The only isolated forest type at Anjanaharibe-Sud is above 1500 m elevation, yet no massif endemics are restricted to this elevational range. The biogeographic conditions that might have encouraged lowland speciation in the Anjanaharibe-Sud region are currently unknown.

A total of 22 species are recorded from Anjanaharibe-Sud, all of which are neither local endemics nor were found at Tsaratanana or Marojejy. These species all have widespread distributions in eastern Madagascar and are restricted to rain forest at low and middle elevations. Their absence at Tsaratanana is readily explained by the

TABLE 7-4. Distribution and endemicity of the Anjanaharibe-Sud Massif herpetofauna.

Species	Distribution		Endemicity	
	Tsaratanana 1500–2876 m	Marojejy 150–2133 m	Anjanaharibe-Sud Massif	Rain forest habitat
AMPHIBIA				
MICROHYLIDAE				
Anodonthyla boulengeri		*		*
Platypelis grandis		*		*
Platypelis cf. *occultans*				*
Platypelis pollicaris	*	*		*
Platypelis tsaratananaensis	*			*
Platypelis tuberifera		*		*
Platypelis sp. 1	*			*
Platypelis sp. 2				*
Platypelis sp. 3			*	*
Plethodontohyla laevipes				*
Plethodontohyla minuta	*	*		*
Plethodontohyla notosticta	*	*		*
Plethodontohyla serratopalpebrosa	*	*		*
Plethodontohyla sp. 1	*			*
Plethodontohyla sp. 2			*	*
Stumpffia grandis		*		*
Stumpffia roseifemoralis		*		*
Stumpffia tetradactyla				*
RANIDAE				
Ptychadena mascareniensis	*	*		
MANTELLIDAE				
Mantella sp. 1		*		*
Mantidactylus aglavei		*		*
Mantidactylus albofrenatus	*	*		*
Mantidactylus asper	*	*		*
Mantidactylus betsileanus				
Mantidactylus bicalcaratus		*		*
Mantidactylus biporus		*		*
Mantidactylus cornutus		*		*
Mantidactylus elegans	*†			*
Mantidactylus femoralis	*	*		*
Mantidactylus flavobrunneus				*
Mantidactylus grandidieri	*	*		*
Mantidactylus grandisonae	*	*		*
Mantidactylus guttulatus	*	*		*
Mantidactylus liber	*	*		*
Mantidactylus luteus		*		*
Mantidactylus opiparis	*	*		*
Mantidactylus peraccae	*	*		*
Mantidactylus pulcher		*		*
Mantidactylus rivicola		*		*
Mantidactylus redimitus		*		*
Mantidactylus ulcerosus				
RHACOPHORIDAE				
Aglyptodactylus madagascariensis	*	*		*
Boophis albilabris				*
Boophis cf. *albipunctatus*				*
Boophis cf. *brachychir*	*	*		*
Boophis erythrodactylus				*
Boophis luteus cf. *septentrionalis*	*	*		*
Boophis madagascariensis		*		*
Boophis mandraka	*			*
Boophis marojezensis	*	*		*
Boophis rappiodes			*	*

Table 7-4. *Continued.*

Species	Distribution: Tsaratanana 1500–2876 m	Distribution: Marojejy 150–2133 m	Endemicity: Anjanaharibe-Sud Massif	Endemicity: Rain forest habitat
Boophis reticulatus	*	*	*	
Boophis anjanaharibeensis			*	
REPTILIA				
GEKKONIDAE				
Ebenavia inunguis		*		
Phelsuma guttata		*		*
Phelsuma lineata		*		
Phelsuma quadriocellata		*		*
Paroedura gracilis		*		*
Uroplatus cf. *ebenaui*	*	*		
Uroplatus sikorae		*		*
CHAMAELEONIDAE				
Brookesia betschi		*		*
Brookesia therezieni				*
Brookesia vadoni				*
Calumma brevicornis	*			*
Calumma gastrotaenia guillaumeti	*	*		*
Calumma gastrotaenia marojezensis		*		*
Calumma malthe	*	*		*
Calumma nasuta		*		
Calumma parsoni				*
Furcifer pardalis		*		
SCINCIDAE				
Amphiglossus melanopleura	*	*		*
Amphiglossus melanurus				*
Amphiglossus minutus				*
Amphiglossus mouroundavae		*		*
Amphiglossus punctatus		*		*
Amphiglossus cf. *tsaratananaensis*	*			*
Androngo crenni				*
Mabuya gravenhorstii	*	*		
Paracontias hildebrandti		*		*
CORDYLIDAE				
Zonosaurus madagascariensis	*	*		
BOIDAE				
Boa manditra		*		
TYPHLOPIDAE				
Typhlops mucronatus		*		*
COLUBRIDAE				
Brygophis coulangesi				*
Geodipsas infralineata		*		*
Geodipsas sp. 1	*			*
Liophidium rhodogaster		*		*
Liophidium sp. 1			*	*
Liophidium sp. 2				*
Liopholidophis epistibes		*		*
Liopholidophis infrasignatus				*
Lycodryas betsileanus		*		*
Pseudoxyrhopus microps		*		*
Pseudoxyrhopus tritaeniatus				*
Pseudoxyrhopus sp. 1			*	*
Total	33	60	5	83

† Data from Blommers-Schlösser and Blanc (1991).

lack of forest below 1500 m; the absence of such a large number of species at Marojejy, however, suggests barriers to dispersal.

Two barriers may have limited dispersal between Anjanaharibe-Sud and Marojejy, the Androranga and Lokoho rivers (including the Andapa basin) to the north and south of the Marojejy Massif, respectively. The only rain forest dispersal corridor that avoids these major rivers is the narrow Betaolana Ridge to the west of Marojejy, which is only 10 km wide in places. The Betaolana Ridge and the Androranga and Lokoho rivers may have acted as a filter, preventing some herpetofaunal species from dispersing into Marojejy. This may also explain the northern distribution pattern of other species, such as the lemur *Indri indri*, which occurs at Anjanaharibe-Sud but is absent at Marojejy. The narrow Betaolana Ridge dispersal corridor may also have isolated the Marojejy Massif sufficiently to account for the evolution of Marojejy endemics.

Conservation

The most vulnerable components of the RS d'Anjanaharibe-Sud herpetofauna are the apparently endemic species restricted to this massif. If their habitats at Anjanaharibe-Sud are destroyed, they may go extinct. The habitat requirements for all five endemic species (and 89% of the massif's herpetofauna) are primary montane forest. Therefore, effective conservation management of the massif depends completely on maintaining primary forest.

Our survey results suggest that faunal differences may exist between the eastern and western sides of the massif. It seems prudent, therefore, to balance conservation efforts so that both flanks of the massif receive equal degrees of protection and management intensity and, if necessary, to include more western forest within the reserve boundary.

The trends in deforestation occurring in and around the RS d'Anjanaharibe-Sud suggest that the lower elevation forest is under the greatest pressure for conversion to agricultural land. The forest below 1100 m elevation shows the greatest signs of degradation and is typically at the periphery of the surviving forest blocks. Our results for the Anjanaharibe Massif demonstrate that most species of amphibians and reptiles are restricted to a narrow elevational range and that the low-elevation forests include 25 species (27% of massif total) that are restricted to below 1100 m elevation and 11 species (12% of massif total) that are restricted to below 950 m elevation (Table 7-1). If current levels of biodiversity are to be maintained, it is critical that peripheral lower elevation forest be protected. Because of the continuing loss of low-elevation forest, conservation efforts at the RS d'Anjanaharibe-Sud must concentrate on protecting this peripheral habitat rather than maintaining the core region of the reserve.

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